Experimental and Applied Acarology **28:** 155–161, 2002.

How specific are host-produced kairomones to host-seeking ixodid ticks?

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Abstract. Ixodid ticks respond to host-produced substances (kairomones) that influence the ticks' host-finding behavior. In the laboratory adult blacklegged ticks, *Ixodes scapularis* Say, lone star ticks, *Amblyomma americanum* L., and American dog ticks, *Dermacentor variabilis* (Say) became akinetic on residues rubbed from their principal hosts (deer for the former two species and dogs for the latter). However, arrestment also occurred when adults of these species were tested using the same method bioassay, but with host substances reversed (i.e., *I. scapularis* and *A. americanum* against canine substances, and *D. variabilis* against deer gland substances). Although adult *D. variabilis* exhibited arrestant responses to deer substances and are often found along trails used by deer, they apparently make little use of deer as hosts. It is unclear whether responding to deer-produced kairomones may have disadvantages for *D. variabilis*. Until the active components of host-produced arrestment kairomones are isolated, identified and evaluated in behavioral tests, this host-finding strategy remains only partially understood.

Key words: arrestant, *Ixodes scapularis*, *Dermacentor variabilis*, *Amblyomma americanum*

Introduction

Finding suitable hosts is critical to the survival and reproduction of three host ixodid ticks. The larvae and nymphs of blacklegged ticks, *Ixodes scapularis* Say, feed on a wide variety of vertebrate hosts from mice and deer to birds and lizards, but most adults feed on *Odocoileus virginianus* (Zimmermann) white-tailed deer (Wilson *et al.*, 1985). The lone star tick, *Amblyomma americanum* L., another three-host species, is also strongly associated with the white-tailed deer (Haile and Mount, 1987) in all feeding stages. In contrast the American dog tick, *Dermacentor variabilis* (Say) feed primarily on rodents as larvae and nymphs, but as adults use medium-sized to large mammals, such as dogs, as hosts. For the adults of two of these tick species, *A. americanum* and *I. scapularis*, deer are the primary, although not exclusive, host species. In contrast, adults of *D. variabilis* feed on several species of large and medium-sized mammals, including horses, but apparently make little use of the increasingly abundant white-tailed deer (Bloemer *et al.*, 1988).

In the laboratory and field, adult *I. scapularis* are known became akinetic on residues of substances rubbed from external glands on the legs of white-tailed deer, (Carroll *et al.*, 1995, 1996), as did adult *A. americanum* in the laboratory. Adults of *D. variabilis* were shown to exhibit similar behavior in response to substances rubbed from the coats of dogs (Carroll, 1999a). However, when adult *I. scapularis* and *A. americanum* were exposed to substances rubbed from canine pelage and adult *D. variabilis* to deer gland substances arrestant behavior occurred (Carroll, 1999b). These adult ticks are capable of traveling ≥ 10 m by their own locomotion and thereby make use of kairomonal cues (Carroll and Schmidtmann, 1996).

The purpose of this paper is to examine and interpret whether apparently broad responses to host-produced kairomones benefit these tick species and what may be the adaptive significance.

Materials and Methods

The methods and results described herein are those reported by Carroll (1999a), and are iterated to enable the reader to understand the general interpretation of chemically mediated arrestment of the three species of ticks by host-produced kairomones in the Discussion.

Ticks

Adult ticks were captured by flagging in Maryland and maintained in plastic vials. *Ixodes scapularis* were kept 6°C, ≈99% R.H., and a photoperiod of 11:13 (L:D) h, *A. americanum* and *D. variabilis* at 22°C, ≈95% R.H., and a photoperiod of 16:8 (L:D) h. Bioassays were conducted those periods when adults of these species were seeking hosts in nature.

Kairomones

Deer leg gland substances were obtained from freshly hunter-killed deer by excising the gland and associated pelage, avoiding contamination of the pelage with blood, or by removing the lower portion the leg at a point just above the tarsal gland. The glands were immediately sealed in plastic bags and frozen at −15°C. Because adults of the three species of ticks seek hosts in the spring (adult *I. scapularis* also seek hosts in the fall), the samples used were from deer were taken in March and April under a Crop Damage or Wildlife Permit issued by the Maryland Department of Natural Resources. Canine samples were obtained by rubbing clean glass rods (12 cm long, 0.3 cm diameter) on the dorsum of dogs' ears. The rods were placed in plastic bags and frozen. The dogs were a German shepherd, a collie and pit bull.

Arrestant bioassay

A capillary tube that had been rubbed between the fingers of a vinyl-gloved hand that had rubbed the pelage of a host animal was inserted vertically into one end of a rectangular block of modeling clay that extended along the diameter of a plastic petri dish (3.5 cm diameter, 1 cm high). At the opposite end of the block was inserted a capillary tube that had been rubbed between the fingers of a clean vinyl glove. A slightly modified version of the bioassay replaced the capillary tubes with glass rods, one that was rubbed in host pelage and the second a clean glass rod. Water was added to the petri dish, which was placed in a larger petri dish (10 cm diameter, 1.5 cm high), also containing water. The nested petri dishes were placed in Plexiglas glove box (65 by 85 by 45 cm) that contained water ≈1 cm deep. A tick was released on the clay block midway between the capillary tubes (rods). The water confined a tick to the clay block and rim and sides of the petri dish (depicted in Carroll, 1998) and maintained a R.H. of ≈95%. The location of the tick was recorded 1, 18 and 24 h after its release on the clay block. Ticks were tested in groups of 10 ticks (one tick per petri dish) at time in the glove box. Data were analyzed using chi-square 2×2 contingency tables with responses of each tick considered independent.

Results

At 1 h after their release on the clay blocks, adult *I. scapularis*, *A. americanum* and *D. variabilis* were still crawling on the clay, the rim of the petri dish and up and down the capillary tubes or glass rods, regardless which of the kairomonal substances was being tested. However, at 24 h after their release on the clay blocks, significantly more ($\chi^2 = 20.0$, $P < 0.005$) adults of *I. scapularis* became akinetic on capillary tubes rubbed with substances associated with tarsal glands of white-tailed deer, than on capillary tubes rubbed with clean gloves (Table 1). Adult *A. americanum* and *D. variabilis* of both sexes showed an arrestant response to deer tarsal gland substances ($\chi^2 = 14.0$–18.4, $P < 0.005$). Both female and male *D. variabilis* of both sexes became akinetic in the presence of substances rubbed from the dorsal surface of dogs' ears ($\chi^2 = 9.0$ and 21.7, respectively, $P < 0.005$). When exposed to substances rubbed from the dorsal surface of dogs' ears adults

Table 1. Percent of adult ticks that exhibited an arrestant response to substances rubbed from deer tarsal glands and the dorsal surface of dogs' ears in laboratory bioassays

Kairomone source	*I. scapularis*[a]	*A. americanum*		*D. variabilis*	
	Female	Male	Female	Male	Female
Deer tarsal gland	90.0[b]	83.3	90.0	83.3	90.0
Dorsum of dog ear	83.3	93.3	86.7	93.3	76.7

[a] Thirty ticks of each sex of each species tested separately against each kairomone source.
[b] For all combinations significantly ($P < 0.005$) more ticks were on treated rod or capillary tube than on control rubbed with a clean glove.

of both *I. scapularis* and *A. americanum* became akinetic ($\chi^2 = 18.5$–21.7, $P < 0.005$) (Table 1).

Discussion

Adult *I. scapularis*, *A. americanum* and *D. variabilis* will feed on any of several host species, and this catholicity is reflected in the results of the bioassays, in which these ticks exhibited an arrestant response to kairomonal substances from the primary host species and a second species. Thus, if an adult *I. scapularis* is picked up by a dog rather than a deer, it is not purely by chance, because the tick may have selected an ambush location on a stem previously brushed by a dog. Two possible explanations of how the host-kairomone-tick system operates are diagramed on Figure 1. First, there could

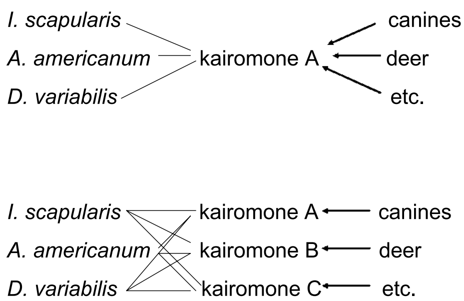

Figure 1. Two possible ways by which host-produced kairomones affect ticks. Above, one kairomone is produced by a variety of hosts, and recognized by a variety of ticks. Below, each host species produces a different kairomone, and each tick species is capable of recognizing multiple kairomones.

be a single compound (or group of compounds constituting a kairomone) produced by dogs, deer and probably other hosts to which the three species of tick respond. An example of this type of system is carbon dioxide exhaled during respiration by all vertebrate hosts. Many species of ticks are attracted to carbon dioxide or exhibit some form of host acquiring behavior, such as leg extension. Second, each species of tick has the ability to respond to a kairomone peculiar to each host species. For instance, *A. americanum* responds to a kairomone produced by dogs that is chemically different from the deer kairomone to which it responds. There tends to be an economy in nature, but a tick is not limited to depending on a single chemical cue. Adult male *I. scapularis* seem to exhibit increased locomotory activity and changes of direction in the presence of substances from deer interdigital glands, but eventually become largely akinetic on the substances (Carroll *et al.*, 1998). Until the active components of these kairomonal substances are isolated and identified, the issue regarding this sort of specificity will remain unresolved. Dobrotvorsky *et al.* (2000) found that *I. persulcatus* nymphs were attracted to polar and low polar fractions of extracts from canine hair, which suggests that the canine kairomone may be a blend of compounds.

By recognizing and waiting on residues rubbed from hosts onto vegetation or the substrate, a tick improves its odds of contacting a suitable host. Because many animals, such as deer, frequent certain feeding and bedding areas, and trails, the presence of a host-produced residue or waste product is often a predictor that animals will regularly return. To use kairomonal cues to aid in acquiring suitable hosts is of adaptive value to ticks in that it increases the likelihood that they will survive to reproduce successfully.

Being enabled to contact deer and canines seems clearly beneficial to *A. americanum* and *I. scapularis*. However, with adult *D. variabilis* it is not clear whether contacting deer benefits these ticks, since they seem to make little use of deer as hosts. Bloemer *et al.* (1988) did not find any adult *D. variabilis* on white-tailed deer that were captured in an area where *D. variabilis* were common at a time of the year when these ticks were seeking hosts. The lack of specificity of adult *D. variabilis* in responding to host-produced arrestant kairomones may increase its chance for contacting a host, but may also increase the chance they will be picked up by deer. The consequences of being picked up by an unsuitable host are probably mostly negative, but it is not clear how serious. It may matter little if a tick drops off the unsuitable host a short distance down the trail, but it may be dire to be unable to start to feed and not reach repletion. Host-seeking adult *D. variabilis* have been reported to congregate near mammalian carcasses (Kneidel, 1984; Carroll and Grasela, 1986), and this behavior may help explain the response of *D. variabilis* to deer kairomones. Ticks waiting around a carcass are likely to contact scavengers such as canines and raccoons. Carroll and Grasela (1986) counted nearly 200 adult *D. variabilis* within 2 m of the carcass of a deer that had died during the winter. Compounds generated by decomposition may be an additional source of kairomones.

Host-seeking adult *D. variabilis* are well known for commonly occurring along trails (Newhouse, 1983) and may be attracted to trails (Carroll *et al.*, 1991). Examination of animal prints in soft earth on trails reveals that several species of medium and large mammals use the same trails. A well used trail may be rich with kairomonal residues, and opportunities for ticks that are generalists in their host selection. Therefore, it may benefit adult *I. scapularis*, *A. americanum* and *D. variabilis* to respond to a number of kairomones just to locate a trail with its many users.

Much more needs to be learned about tick behavior and the chemistry of host-produced kairomones before we can adequately understand tick host-finding systems.

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